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IMPROVING EGG PRODUCTION BY BREEDING

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BULLETIN 231.

IMPROVING EGG PRODUCTION BY BREEDING.¹

By RAYMOND PEARL.

It is safe to say that never has there been so keen and widespread an interest in the improvement of poultry in respect to egg production as exists at the present time. All over the world poultry keepers are waking to the fact that some hens lay more than others; that it costs no more to hatch, rear and care for those which lay more; and that they want this sort in their flocks.

There would seem to be little doubt that this awakening is due in considerable degree, at least, to the rapid development during the last ten years of egg laying contests in different parts of the world. We are indebted for the inauguration of such contests on a large scale to the enterprise of the Australians. In recent years we have seen their development in this country. It seems likely that we shall see a much further growth of the laying contest idea in the United States, as well as in European countries. To be sure some writers for the poultry press, who apparently see little or nothing of value in laying tests of any sort, have been predicting that the laying competition has about run its course, and that the end is now in sight; that we are, in point of

¹The substance of this paper was presented as an address to the American Poultry Association at its annual meeting in Atlantic City, August 13, 1913. The address as originally read has been widely published in the poultry press. For some time past the Maine Agricultural Experiment Station has announced that there would be published a popular discussion of the scientific results regarding the mode of inheritance of egg producing ability set forth in Bulletin 205. It has seemed best to meet the demand for such a publication by taking as a basis the Atlantic City address and adding to it such amplifications and illustrations as seem to be necessary. This accordingly has been done in the present bulletin. The fact that the material was put into form originally for the purpose of the spoken address, accounts for the personal style.

fact, witnessing its last decline before utter extinction. Unprejudiced observation, however, would seem to indicate that these contests make a strong appeal to the poultry public. It is difficult to conceive of any single measure better calculated to arouse general interest in poultry keeping and to call attention to the results which follow good care and breeding. In other words, the educational value of laying contests would seem to be beyond question. That they can be so conducted as to contribute to existing knowledge of the laws of egg production also is beyond doubt. I have recently had the opportunity of examining the detailed plans for the conduct of a series of such laying competitions, which are to be undertaken, with government subsidies, in two European countries. There can be no question that these plans, if carried out, will contribute materially to scientific knowledge of the laws of egg production.

Underlying the immediate stimulus afforded by the laying contest are to be found two fundamental reasons for the present interest and activity in the direction of improving egg production. These are:

(a) The poultryman's belief that egg production is an inherited character. In holding this opinion he is certainly correct. One might indeed, say "knowledge" instead of "belief" here.

(b) His belief that any character which is inherited is capable of improvement by intelligent breeding. Again, this belief is entirely well founded, provided only that an exception be made for characters (if there are any such) in which all possible improvement in innate hereditary constitution has already been made.

EGG PRODUCTION IS INHERITED.

To say, as we have above, that "egg production" is an inherited character is not quite enough. This might be taken to mean only the fact that the mode of reproduction characteristic of birds, which is to say reproduction by means of eggs with albuminous and calcareous envelopes—is an innate and hereditarily fixed matter in the fowl. But the poultryman is interested, as well as the investigator in the field of genetics, in something more than this. He wants to know whether the *differences* which he observes in egg-laying capabilities amongst different breeds, or flocks, or finally individuals, are inherited. General observations

indicate to the poultryman that at bottom the foundation of a great many of these differences in laying ability with which he is familiar is heredity. But how? And under what limitations? For plainly this is not a simple matter. If it were, none of our hens now would ever lay less than 200 eggs per annum, except in the case of remote back woods regions, where the gospel of the trap-nest had not yet penetrated. Trap-nest selection of high producers has opened the eyes of the poultryman to one thing certainly, even though it may have obscured his vision in other directions. This thing which is clearest is that all high-producing hens are not equally capable of transmitting this valuable quality to their progeny. So that while it may be perfectly certain that the difference between a 200-egg producer and a 50-egg producer is in some way or other an hereditary difference, we shall not get far towards a practical utilization of this fact until we know something more about its nature.

So, then, the first essential step to be taken towards the improvement of egg production by breeding is to find out the way in which variations or differences in producing ability are inherited. For some six years past considerable attention has been devoted to this problem, with results which have been set forth in detail in a series of papers from the Biological Laboratory of the Maine Agricultural Experiment Station. Of the more recent of these papers is Bulletin 205, which has the title "The Mode of Inheritance of Fecundity in the Domestic Fowl." This bulletin is technical in character. It was not written for the poultryman but for the professional student of genetics. On this account it has apparently not been quite clearly understood by some poultrymen, and the results and conclusions have, in some cases, been misinterpreted. It will be the endeavor here, as briefly as possible, to make clear the essential results of these studies.

FACTS ABOUT INHERITANCE OF FECUNDITY.

First as to the facts: The following are simple statements of the actual results, obtained in trap-nesting Barred Plymouth Rocks and Cornish Indian Games, and all possible sorts of crosses between these breeds, over a period, collectively, of nearly fifteen years. The total number of birds involved in these trap-nesting operations has been large, aggregating, all told, between

five and six thousand individuals. Out of these records, the following facts clearly appear.²

1. The record of egg production of a hen, taken by itself alone, gives no definite, reliable indication from which the probable egg production of her daughters may be predicted. Furthermore, mass selection on the basis of egg laying records of females alone, even though long continued and stringent in character, failed completely to produce any steady change in type in the direction of selection.

2. Differences in egg producing ability are, in spite of the above results, certainly inherited. There are two lines of evidence showing that this is the case. The first is that derived from the general observation that there are widely distinct and permanent (under ordinary breeding) differences in respect to egg laying ability between different races, strains and breeds of fowls. In the second place, a study of pedigree records of poultry at once discovers blood lines in each of which a definite particular degree of egg producing ability constantly reappears generation after generation, the "line" thus "breeding true" in this particular. With all birds kept under the same general environmental conditions such a result can only mean that the character is in some manner inherited.

3. The number of visible oöcytes on the ovary bears no definite or constant relation to the actually realized egg production.

4. This can only mean that observed differences (variations) in actual egg production depend upon differences in the complex physiological mechanism concerned with the development of oöcytes, and the separation of them from the ovary and the body (laying).

For reasons which cannot be gone into fully here on account of lack of space, attention has been focused during the later phases of the study, on winter egg production.

Primarily these reasons are two: first, that winter production is economically the most important in the case certainly of poultrymen in northern latitudes; and second that winter production gives a more accurate and reliable measure of the bio-

²More detailed discussion of these results, together with direct references to the evidence on which they are based will be found in Bulletin 205, pp. 377-391.

logical variable which it is desired to measure—namely the maximum innate ability of the individual to produce eggs—than the record over any longer period.

The first of these points has never been in dispute. Regarding the second there has been a good deal of doubt on the part of some students of trap-nest records. They argue that because they find now and then a case which seems to them an exception to the general rule that the pullet winter production is correlated with total production, that therefore winter production is not a reliable measure of fecundity. It is pointed out that a bird which produces no eggs, for example, in her pullet winter period sometimes makes a very high two year or three year record.³ This may certainly happen but it has no particular bearing on the general point at issue. There seems to be a misunderstanding or confusion of thought more or less widely prevalent with reference to what it really is that one *wants* to measure by means of trap-nest or milk scale, as a guide to breeding operations. I may perhaps make the point here clearer by concrete illustration. Any poultryman knows that by damp, dark, unventilated houses, unpalatable and improper food, fed in insufficient amount he can prevent the finest laying strain in the world from producing many eggs. Yet clearly no one would accept a trap-nest record made under such circumstances as measuring the bird's inherent capacity as a layer. What it is really desired to know about, however, is just this *inherent capacity*. One wants to be able to know, that, for example hen A is a good layer, while hen B is a poor layer, *when both are under the absolutely most favorable circumstances for egg production* in every particular, so that full opportunity shall be given for every innate inherited *potentiality* to come to actual, visible expression. But plainly the longer the time unit chosen for the record, the more impossible it becomes even measurably to approach the continued realization of the "absolutely most favorable conditions" for egg produc-

³But why stop at two or even three years? *Every single one of the arguments* to the effect that a three year record is a "better" measure of a hen's fecundity than her pullet winter record, can, *with even greater force*, be used to defend the thesis that a twenty year record is a "better" measure than a three year one, hens having been known to produce eggs up to that age.

tion. The shorter the time unit the more nearly possible will it be to realize these conditions over the period of the test. It is, in this regard, exactly with the hen as with the cow, where the recent researches of Gavin⁴ as well as those of Wilson,⁵ have demonstrated most clearly that the most adequate time unit for the measurement of a cow's innate milk producing ability taking all things into account is *not* the year test, nor the 30 days test, nor even the 7-day test, but the *one* day test when production reaches its maximum. This (revised as suggested by Gavin) gives us the measure of what each cow is hereditarily and physiologically *capable* of doing if the attendants, the weather and every other external relation, will do their parts.

We have then to choose a particular short period for getting our reliable measure of a hen's fecundity. Why take winter production? Because, in a word, it is in this period that the *differences* in innate reproductive capacity between different individuals are most strongly marked.⁶ It is probable that a shorter and earlier period would furnish a still better measure of innate fecundity than the winter period, particularly as the environmental conditions in mid-winter are not the best. For practical purposes, the poultryman who operates his trap-nests after the fall and early winter months, is paying a high price for knowledge which is of very little use to him from the

⁴Gavin, W. The Interpretation of Milk Records. Jour. Roy. Agr. Soc., Vol. 73, 1913.

Studies in Milk Records: The Influence of Foetal Growth on Yield. Jour. Agr. Sci., Vol. V, 1913, pp. 309-319.

Studies in Milk Records: On the Accuracy of Estimating a Cow's Milking Capability by Her First Lactation Yield. *Ibid.* Vol. V, pp. 377-390, 1913.

⁵Wilson, J. The Inheritance of Milk Yield in Cattle. Proc. Roy. Dublin Soc., Vol. XIII, pp. 89-113, 1911.

The Elimination of the Unprofitable Cow. Jour. Dept. Agr., Ireland, Vol. XIII, No. 4, 1913.

⁶It may be noted here that the writer's conclusions on the above point have been independently confirmed by Professor James Wilson and Miss Murphy, working upon Irish laying records (cf. Jour. Dept. Agr. Ireland, Vol. XIV, No. 2). The results of the English Utility Poultry Club's 12-month laying competition at Harper-Adams College also show clearly the importance of the early fall and winter laying as a measure of innate fecundity.

breeding standpoint. The intelligent breeder trap-nesting his flock not over three months in the year, can make practically just as rapid progress in breeding for increased egg production as his neighbor who trap-nests twelve months in the year.

To return from this digression to the main line of discussion, it will be remembered, then, that in what follows reference will be to *winter* egg production unless the contrary is specifically stated.

5. It is found to be the case that birds fall into three rather well-defined classes in respect to winter egg production. These include (a) birds with *high* winter records, (b) birds with *low* winter records, and (c) birds which do not lay at all in the winter period. The division point between *a* and *b* for the Barred Plymouth Rock used in these experiments falls at a production of about thirty eggs.

The next step is to inquire for each of these classes separately how egg producing ability is inherited within the class. We may first deal with high production.

6. High productiveness may be inherited by daughters from their sire, independent of the dam. This is proved by a mass of detailed evidence, presented in the complete paper. This evidence consists of the results of mating after mating, in which the same proportions of daughters of high laying ability are produced by the same sire, whether he is mated with dams which are poor layers or with dams which are high layers.

7. High laying ability is *not* directly inherited by daughters from their dam. This is proved by a number of distinct and independent lines of evidence, of which the most important are: (a) that continued selection of high producing dams does not alone alter in any way the mean egg production of the daughters. If an alteration does appear in any case following such selection, further analysis shows that some additional element other than the dam's egg record came into account in making the selections of breeders. (b) The proportion of high producing daughters is the same whether the dam is of high or of low fecundity, provided both are mated to the same male; (c) the daughters of a high producing dam may be either high layers or poor layers, depending upon their sire; (d) the proportion of daughters which are medium or poor layers is the same whether the dam is a high or a poor producer, provided both are mated to the same male.

8. Mediocre or poor laying ability may be inherited by the daughters from either sire or dam, or both.

Now, all of these eight points are merely statements of fact. They are the results which any intelligent person who examined our extensive trap-nest and pedigree records would be bound to reach. They depend in no way upon any "theory" of inheritance. I can assure those to whom Mendelism is as the proverbial red rag to the bull that nothing which has been said so far is even to the slightest degree tainted with this dreadful (?) doctrine.

SUGGESTED MENDELIAN INTERPRETATION OF FACTS.

An isolated fact does not alone contribute to the body of organized knowledge known as science. Its relation to other facts must first be understood. Now, the facts regarding egg production which have been set forth above, do, as a matter of fact, accord in a remarkably clear manner with a Mendelian interpretation of the inheritance of fecundity in the fowl. Such an interpretation has been worked out in detail in Bulletin 205. Through this interpretation this isolated group of facts is brought into relation with a much wider range of facts about inheritance in poultry and other animals. In this way we are better able to understand (in light of present knowledge) the meaning of our facts, and, on this basis, make plans for investigations which shall take us again a little farther into the realm of the unknown, beyond the boundaries of our present knowledge.

But what is the good of all this? How is it going to help John Smith to win the first prize in an egg laying competition? It must be said at the outstart that, much to my regret, neither the facts nor their Mendelian interpretation, will furnish any neat little rule-of-three whereby all John Smiths can win all first prizes. Successful poultry breeding will continue in the future, as it has in the past, to demand a lot of intelligence, thought, skill and rationally directed effort. I hope and believe, however, that the results discussed above may be of some help in efforts to improve egg production by breeding. It is farthest from my desire to claim too much for them, but I do think they help us a little in certain general directions. In the first

place these results, by showing that the inheritance of egg producing ability is not a simple, uncomplicated transmission of something from dam to daughter without change, make it somewhat easier to bear the disappointments which attended devotion to the gospel of the trap-nest, in its original inspirational form. In the second place, they help us to make a more just and adequate distribution of emphasis on the different basic elements of a systematic plan for the improvement of poultry in egg production. Finally, by furnishing a generalized mode of interpretation of observed results, or in other words, by giving a clearer and broader *understanding* of how egg production is inherited, these results help us to interpret, and profit in our own breeding operations by the experience of others.

It would be very easily possible to make out a system of matings, on the basis of the results of Bulletin 205, showing in great detail how to proceed towards building up a laying strain. Indeed, such specific plans have been worked out by a number of my friends. I have refrained from doing this, however, because it seems to me to be of doubtful practical utility. Lest I should seem to be repudiating both my results and my friends, let me hasten to give the reasons for this doubt. The reasons are general in character and are found in the fact that such schemes of mating are essentially *mechanical*, whereas both the things to be bred in accordance with the scheme (the fowls), and those who are to carry out the plans (the poultryman) are essentially *living*. Perhaps in final analysis the basis of life may be mechanistic, but certainly living things do not in practical every day life behave with that precision and definiteness which we expect from a machine. Being a little acquainted with the frailties of both poultry and poultrymen, I am not too optimistic as to the outcome of trying to breed chickens by formula.

A PLAN FOR THE PRACTICAL BREEDER.

It seems to me that possibly it may be more helpful to draw out from these results some general principles in breeding for egg production, which every poultryman can apply. What then are the basic elements in a well-directed effort towards the improvement of poultry in egg production by breeding? I should put them in this way.

1. Selection of all breeding birds *first* on the basis of *constitutional vigor and vitality* making the judgment of this so far objective as possible. In particular the scales should be called on to furnish evidence. (a) There ought to exist, for all standard breeds of fowls, normal growth curves, from which could be read off the standard weight which should be attained by a sound, vigorous bird, not specially fed for fattening, at each particular age, from hatching to the adult condition. These curves we shall sometime have. (b) Let all deaths in shell, and chick mortality, be charged against the dam, and only those females used as breeders a second time which show a high record of performance in respect to the vitality of their chicks, whether in the egg or out of it. This constitutes one of the most valuable measures of constitutional vigor and vitality which we have. If for no other reason than to measure this breeding performance, a portion of the breeding females each year should be pullets. In this way one can in time build up an elite stock with reference to hatching quality of eggs and viability of chicks. (c) Let no bird be used as a breeder which is known ever to have been ill, to however slight a degree. In order to know something about this, why not put an extra leg-band on every bird, chick, or adult, when it shows the first sign of indisposition? This then becomes a permanent brand, which marks this individual as one which *failed*, to a greater or less degree, to stand up under its environmental measures of constitutional vigor. (d) Many of the bodily stigmata by which the poultryman, during the last few years, has been taught to recognize constitutional vigor, or its absence, have, in my experience, little if any real significance. Longevity is a real and valuable objective test of vigor and vitality, but it is of only limited practical usefulness, because of the increasing difficulty with advancing age of breeding successfully on any large scale from old birds of the American and other heavy types.

2. The use as breeders of such *females* only as have shown themselves by trap-nest records to be high producers, since it is only from such females that there can be any hope of getting males capable of transmitting high laying qualities.

3. The use as breeders of such *males* only as are known to be the sons of high producing dams, since only from such males can we expect to get high producing daughters.

4. The use of a pedigree system, whereby it will be possible at least to tell what individual male bird was the sire of any particular female. This amounts, in ordinary parlance, to a *pen* pedigree system. Such a system is not difficult to operate. Indeed, many poultrymen, especially fanciers, now make use of pen pedigree records. It can be operated by the use of a toe-punch. All the chickens hatched from a particular pen may be given a distinctive mark by punching the web between the toes in a definite way. If one desires to use a more complete *individual* pedigree system, he will find the system described in Bulletin 159 of the Maine Agricultural Experiment Station a very simple and efficient one. It has been in use at this Station for seven years, with entire satisfaction, on the score of both accuracy and simplicity.

5. The making at first of as many different matings as possible. This means the use of as many different male birds as possible, which will further imply small matings with only comparatively few females to a single male.

6. Continued, though not too narrow, *inbreeding* (or line breeding) of those lines in which the trap-nest records show a preponderant number of daughters to be high producers. One should not discard all but the single best line, but should keep a half dozen at least of the lines which throw the highest proportions of high layers, breeding each line within itself.

Items 4, 5, and 6 imply the carrying over of a considerable number of cockerels until some judgment has been formed of the worth of their lines, through the performance at the trap-nest of their sisters.

Item 6 assumes, as an absolutely necessary prerequisite that item 1 will be faithfully and unfailingly observed.

Some indication of the manner in which the application of such a plan of breeding as that outlined will work out is given in Figs. 74, 75 and 76. These figures show, in a diagrammatic manner, the results of mating male birds of different hereditary constitutions with respect to egg laying capacity, with females which have been shown by the trap-nest to be high producers. In these diagrams different geometrical patterns are used to indicate, in the case of the female performing ability, and in the case of the male the ability to transmit high laying quality to his progeny.

In accordance with the paragraph numbered 2 above only females will be used by the practical breeder which have been shown by trap-nest records to be high producers. All such females will, in the terminology used in Bulletin 205, fall in either Class 1 or Class 2 of females. In the diagrams a high producing female is shown in solid black; a mediocre or low producer (female) is indicated by fine cross-hatching; a very poor producer, which lays few eggs in its lifetime and *none at all* in the winter period, is indicated by a mere outline without any filling whatever.

It is shown in Bulletin 205 that there are nine different types of males, with respect to inherited qualities of egg production. These are numbered in order 1 to 9. In the diagrams the results of mating each one of these nine different types of males with a flock of high laying hens is shown. In making these diagrams it is assumed that one-half of the flock of high laying females will be Type 1 females and one-half will be Type 2 females, as described on page 306 of Bulletin 205. This is a fair assumption from the practical standpoint. By trap-nest records alone the breeder cannot tell whether a given high laying bird is of Type 1 or Type 2. He can only judge of this from her progeny. Experience indicates, however, that about one-half of all high laying birds will fall in one of these types and one-half in the other. It is assumed in the diagrams that each pair of parents will produce 32 off-spring, of which 16 will be males and 16 females.

The way in which the diagrams are to be read may be illustrated by a particular example. Let us consider Mating C. We have here the mating of a Type 3 male bird with the high laying flock of females, as indicated by the solid black hen. This mating produces a flock in which nearly all the females (14 out of 16) are high layers. Two out of 16 are mediocre layers (poor winter producers). Three different kinds of male birds are produced from this mating. Six out of the 16 are of Type 1, as indicated by the solid black bird. 8 out of 16 are of Type 3 like the sire, and 2 out of 16 are Type 7 males, indicated by very narrow bars. Now if a breeder gets from a mating of some particular male with a flock of high laying hens, which he has selected by the use of the trap-nest, a flock which is made up of different sorts of producers in about

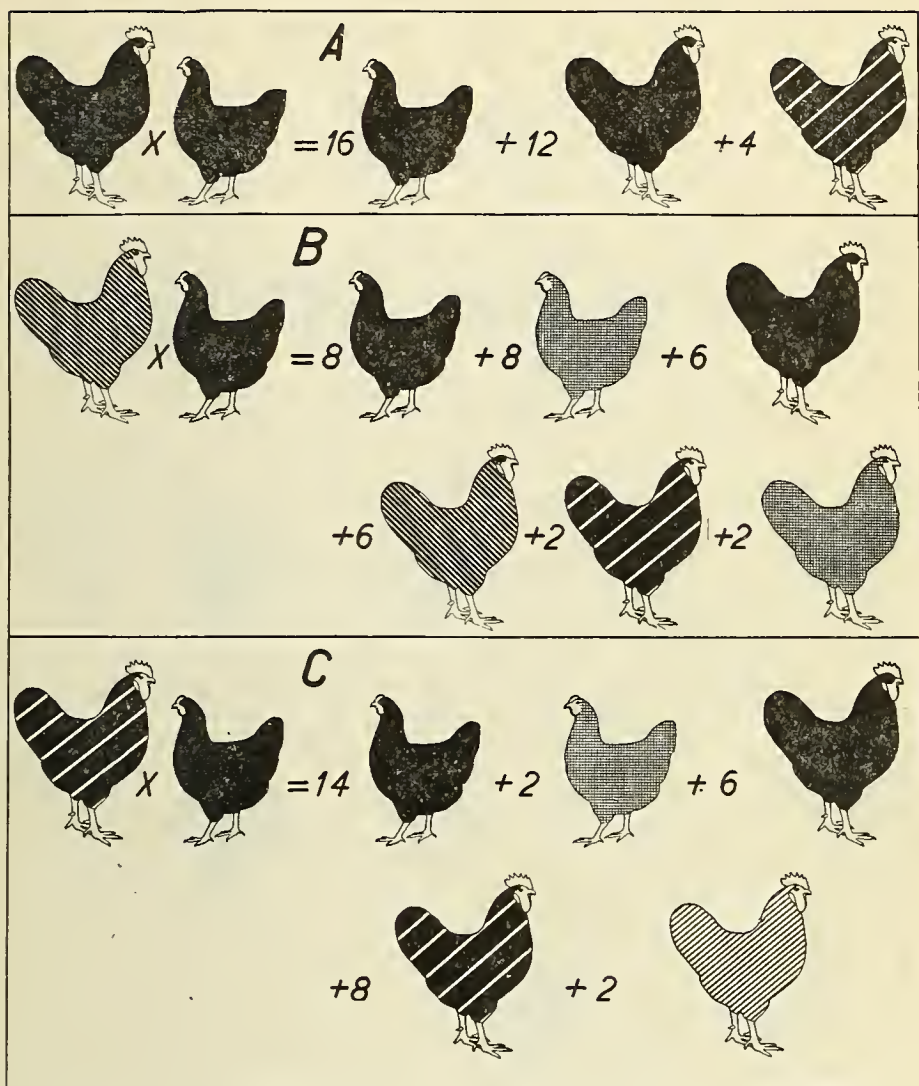


Fig 74. Diagrams showing the results of matings: A, a Type 1 male; B, a Type 2 male; and C, a Type 3 male, with high laying hens. In these and the following diagrams, a solid black hen means a high winter producer, a cross-hatched hen a low winter producer, and a clear white hen a zero winter producer.

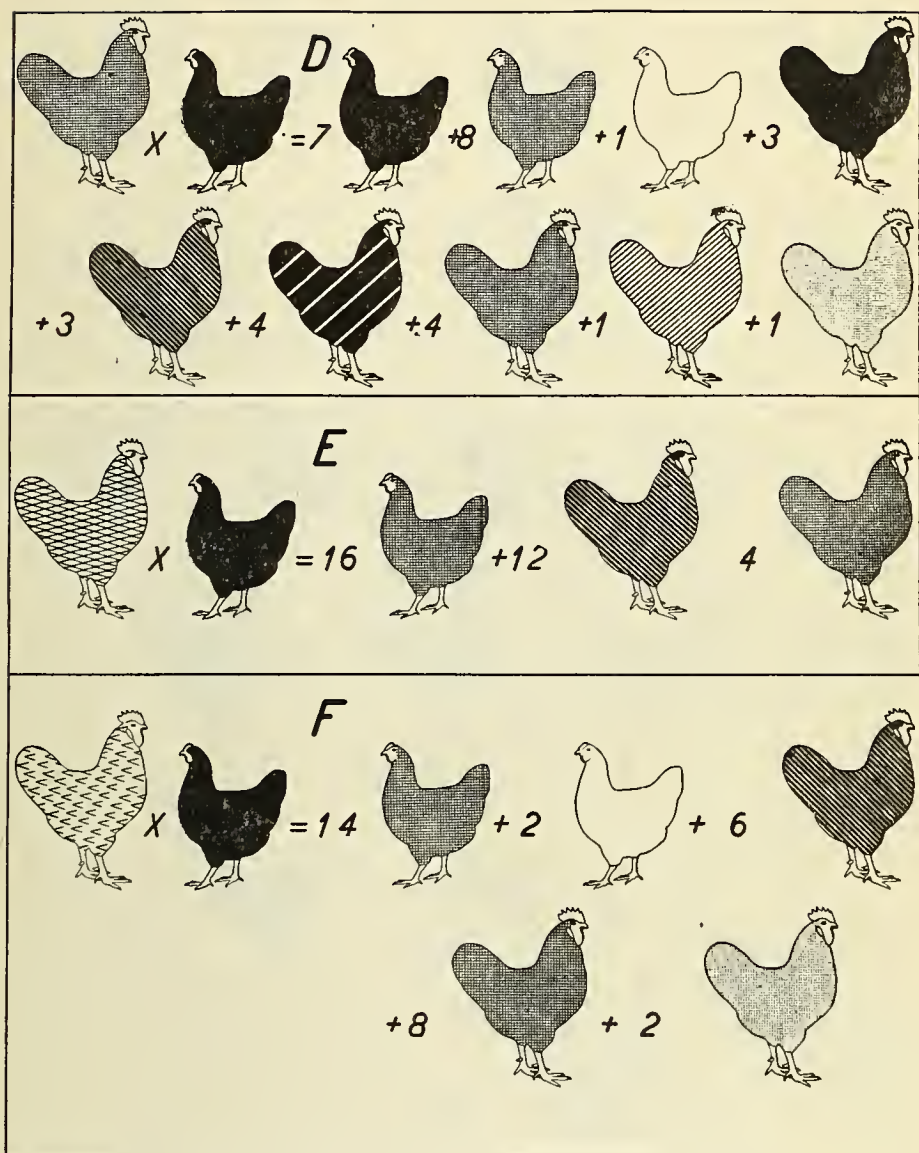


Fig. 75. Diagrams showing the results of mating: D, a Type 4 male; E, a Type 5 male, and F, a Type 6 male, with high laying hens.

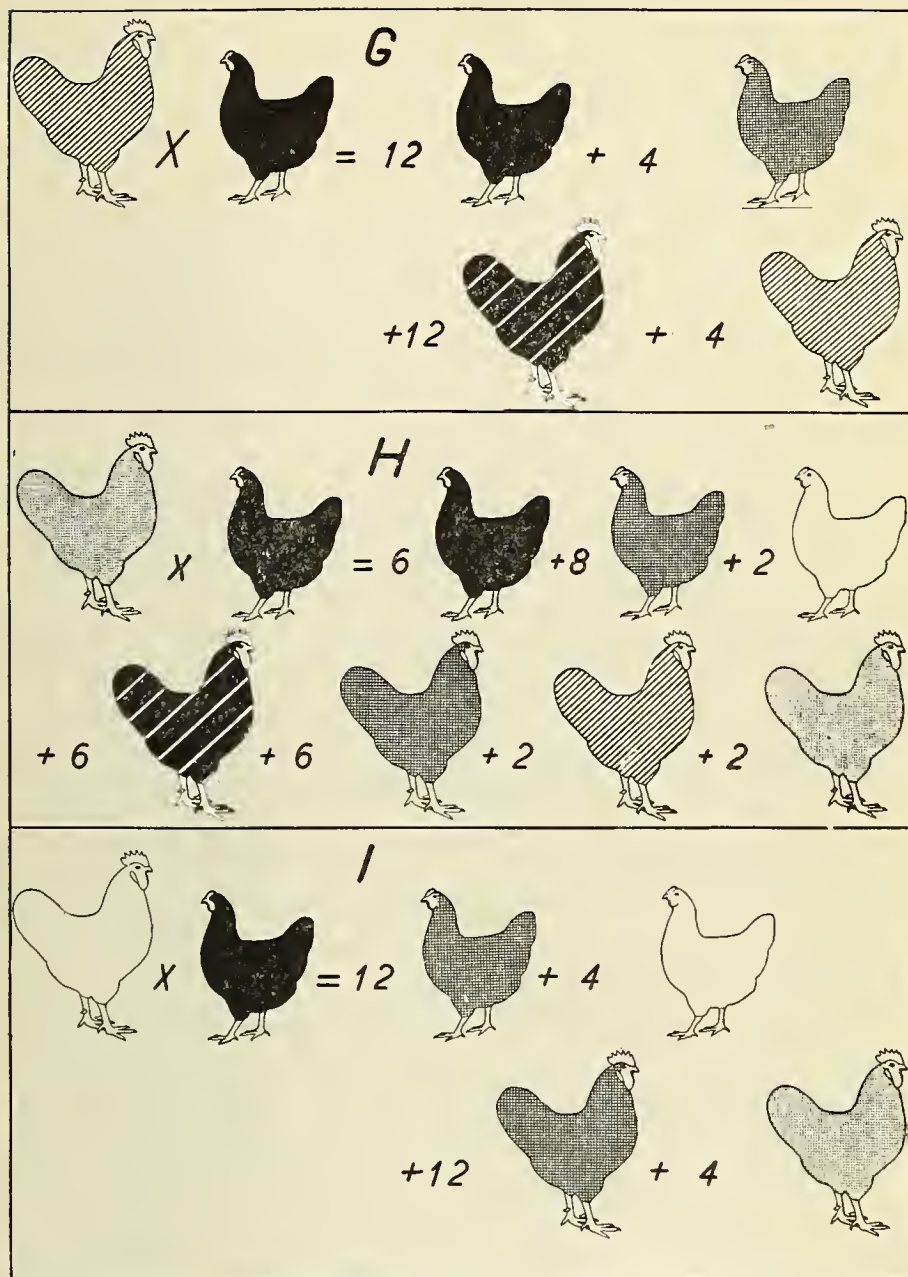


Fig. 76. Diagrams showing the results of mating: G, a Type 7 male; H, a Type 8 male; and I, a Type 9 male, with high laying hens.

the proportions indicated in Fig. 1, Mating C; that is if about $\frac{1}{4}$ of the pullets are high producers, he may conclude with great probability that the sire he used was a Type 3 male, and that he will do well to use the brothers of the high laying pullets as breeders next year. In other words, the proportion of pullets of different laying capacities furnishes the guide to the breeder as to the probable hereditary constitution of their sire, and furthermore serves as a guide to him as to what male birds to select for use the following year. Of course this implies that one will carry over during the winter a larger number of male birds than is customarily the case. This is rather important since our only guide to the probable worth of the males, at least at the outstart, is through the performance of their sisters and their dams.

We may contrast the results shown in the mating just described with the results shown in Mating H, Fig. 3 which is of a Type 8 male with the flock of high producing hens. Here we see from the diagram that there are produced all three sorts of pullets—high producers, mediocre producers (under 30 winter producers), and very poor producers (zero winter layers). These are in the proportions indicated in the diagram—namely 6 high layers to 8 mediocre to 2 poor. An examination of the male part of the equation shows that here we have 6 Type 3 males and 6 Type 4 males and two each of Types 7 and 8. This is a flock of distinctly different constitution than the one described before. It is clear that some of the males from this family will be nearly worthless as breeders for improved egg production in succeeding generations.

In making these diagrams the following general rule has been followed for the practical guidance of the breeder. Males which are desirable to use as breeders for egg production are indicated either by a solid black or a barred pattern, and in the case of birds with the barred pattern the more black in the pattern the more desirable the birds are as breeders for egg production. With this general rule in mind the intending breeder for increased egg production will find it of interest to study these diagrams and compare them with the results obtained in his own breeding, when he keeps any sort of pedigree system even such as that described in paragraph 4 above.

The first question which will occur to the breeder's mind is as to whether there are any external characters by which the nine different types of males can be distinguished one from another. Unfortunately no such external criteria have yet been discovered. If it could be done it certainly would be of a great aid in breeding for egg production. The only way that we know now, however, by which it is possible to form a judgment as to a male bird's innate, inherited qualities in respect of egg production is through his progeny. We must find out what his daughters do. Then the proportion of mediocre layers and poor layers amongst his progeny furnish at once a clue as to his probable composition. The diagrams show how one may form this judgment.

One interesting point brought out by the diagrams is that, with the exception of a Type 1 male (Fig. 74. A), the mating of any sort of male with high producing hens *only*, results in a flock of male offspring of better average quality, taken as a whole, than the sire himself. In other words, the use of high producers, proven by the trap-nest, as the *only* females for breeding purposes, "grades up" very rapidly the cockerels produced.

The whole system of breeding here outlined is an application, in the simplest form possible of two principles, one general and the other special to the present case.

The first is the general principle of *the progeny test in breeding for performance*. This is the principle which has led the plant breeder to such notable triumphs during the last fifteen years. In my judgment no system of breeding for performance in animals not fundamentally based upon it will ever achieve any permanent success. The second principle, is *the recognition of the significance of the male in breeding for egg production*. It has been the custom in trap-nesting work to reckon pedigrees in the female line only. This we can now see to be an essentially futile procedure, so far as concerns the daughters. To say that "this pullet is the daughter of Lady Splendissima (with a tremendous record)" is perhaps good advertising. It, however, conveys no information of any special value to the breeder, until he knows who was the Lady's consort in this particular reproductive venture.

In closing conviction may be expressed that the plan of breeding for egg production set forth, which involves nothing in principle or practice which any poultryman cannot put into operation, will not fail, if consistently and intelligently followed for a period of years, to bring about a material increase in the productiveness of the flock. The evidence which leads to this conviction is the best of all evidence; the plan has been tried and it works.